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# Sub-epidermal rusts.

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(WITH PLATE XV.)

During the past year I have made a structural study of the teleutosporic stage of *Puccinia coronata* Cda. and *P. rubigo-vera* DC. upon different hosts with the hope that careful work would reveal, among other things, some differentiating structural characteristics. To be of worth, such defining marks must be constant through all variations of an individual species. Though the work was not wanting in interest, it may be well to say that, with regard to the discovery of such diagnostic features, my observations have been essentially negative; for structural variations which upon some hosts were often quite marked were upon others either absent or so slight as to be of no comparative value.

In most species of Uredineæ, the teleutospores break through the epidermis of the nourishing plant (fig. 1), but in both the species mentioned they reach maturity in the matrix or sorus without rupturing the enclosing epidermis (fig. 2), a condition which is typical of a number of other species, which, for convenience in this paper, have been termed "sub-epidermal."[1]

These species, because of their similarity of development, present many common peculiarities of form and structure. In some cases, as P. coronata and P. rubigo-vera, species grade the one into the other so closely as to nearly defy separation upon a structural basis. Upon examining type spores of these two forms, one immediately notices the striking differences in the apices, P. coronata being possessed of a crown of flame-yellow finger-form projections, while those of P. rubigo-vera are truncate (fig. 13 and 12, *a* and *b*). These, however, are not constant characteristics. Some specimens of P. rubigo-vera produce teleutospores which show a strong tendency to form points, and many specimens of P. coro-

[1] P. scirpi DC. †; P. eleocharidis Arth. †; P. striatula Peck †; P. vulpina Schroet. †; P. anemones-virginianæ Schw. †; P. galiorum Lk.; P. sessilis Schneider; P. obscura Schroet. †; P. phalaridis Plow.; P. poarum Nielson. The species marked (†) were studied in connection with this paper.

nata develop spores but few of which show any signs of the, digitate processes.

Forming within the host as these spores do, they are under constant pressure because of their own growth and the resistance of the host tissues; hence it is that we may expect to find a large number of malformations. In all the sub-epidermal species studied one-celled forms (figs. 12 *f*, 13 *g*) were found aggregated in the same pustules with the regularly formed teleutospores, but cross sections, vertical to the surface of host, always found them to be located around the borders of the sorus or in places in which an upward expansion was not permitted.

As I did not in any case observe mature spores of this form in portions of the sorus in which there would be freedom of expansion, and as such spores are often found in sori of P. graminis and other eruptive species, which for some reason have failed to tear away the epidermal covering, I take it that these spores are simply dwarfed forms due, perhaps, to a lack of nourishment and excessive pressure at the proper time for the formation of the cross septum. According to this view of formation the term "mesospore"[2] used either according to Sorauer or Dietel is not applicable to these anomalies as found in the species studied (foot-note 1).

As the number in which they appear in relation to the perfect spores is exceedingly variable, not only upon different hosts but in different pustules on the same host, I deem it more probable that their occurrence in these species is due more essentially to local conditions of development than to any hereditary tendency.[3] Certain it is that pressure within the crowded sorus is capable of producing an almost unlimited number of irregularities in the spore forms. Such forms as the one seen at *f*, fig. 13, are always to be found in the borders of the sori, the curvature being due to continued pressure exerted by more internally forming spores. Furthermore, the typical spores of a species are found to arise from the central area of the spore-bed, the position in which the spores

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[2] Winter—Rabenhorst's Kryptogamen Flora, Pilze, vol. i, p. 133.

Sorauer—"Between the uredo and teleutospores one often observes intermediate forms (mesospores) which are really to be considered as simple transition forms." Pflanzenkrankheiten, ed. 2, vol. ii, p. 213.

Dietel—"These spores (mesospores) are not medial between two other spore forms; but the species in which they occur stand themselves intermediate between the two genera, Uromyces and Puccinia." Morphologie und Biologie der Uredineen, p. 6; Botanisches Centralblatt, vol. xxxii, 1887.

[3] This is not given as an explanation of the production of the mesospores as found in such species as *P. vexans* Farlow and *P. sporoboli* Arth., which I have not studied.

are least subjected to irregularites of resistance. In every case the pressure is due to enlargement of the spore during growth, while the adjacent spores and the surrounding tissues, simply through resistance, constitute the moulds which shape the irregularities.

These irregularities in the spores are of two distinct natures, those which arise from an actual moulding of the spore form due to turgidity of growth and inequalities of external resistance and those which are due to an innate molecular condition of the spore wall which permits of inequalities of extension. The latter mode of formation is of an hereditary nature, due to peculiarities of molecular structure effected by the protoplasm of the species in which it occurs; the first is an accident of development.

Herein lies what I take to be the chief structural difference between the species P. coronata and P. rubigo-vera. While the digitate processes upon the spores of the first are normal to the particular parts of the spore membrane, the irregularities in the contour of the spores of the latter are accidental, depending for the particular forms upon the moulding of the young spores and a subsequent thickening of the cell walls.

That the points upon the spores of P. coronata have no constant regularity of form, number or position, does not invalidate this idea. Certain portions of the spore membrane are possessed of greater powers of extension, perhaps by imbibition, and they expand in the direction in which there is least resistance. These points are always to be seen in vertical sections of the sorus extending into depressions in the epidermis and into interstices between the apices of the spores. The position of the points with reference to the spores, as seen from above, is shown in fig. 5.

The Stroma.—In those species in which the teleutospores are truly sub-epidermal during their whole development, they are not formed upon the same spore bed as the uredospores, which necessarily rupture the epidermis, but are aggregated in a new spot under the uninjured epidermis. It is in the completion of this new sorus that the fungus displays a high degree of parasitism in that, when mature, the mat of fungal tissue which surrounds the spores becomes essentially a part of the host. The fungal hyphæ ramify in the host tissues, principally by way of the intercellular spaces (figs. 2, 3 and 4). When a fruiting spot is formed two or more hyphal branches coalesce, as seen in fig. 3, in an intercellular space lying between the epidermis and the hypodermal layer. This is the beginning of the *stroma*[4] (hymenium, sporenlager, spore-bed, etc.), a mass of fused fungal hyphæ from which the spores arise.

In section, the mature stroma gives the appearance of a regular tissue displaying many large cell-like openings often much larger than the diameter of the ordinary hypha, due to the interstices between uniting filaments and the solution of some of the uniting walls (figs. 2 *b* and 11 *c*).

The fungal filaments not only have the power of uniting themselves with the cell walls of the host by fusion, but probably by the secretion of an unorganized ferment,[5] can penetrate, pass through or wholly dissolve them. Hence it is that the hypodermal host tissues are always to be found closely united (fused) with the stroma and are not distorted, though the pustule, since its formation, has expanded greatly. This quality of fusion is most noticeable in the so-called "paraphyses" which accompany the teleutospores of P. rubigo-vera.[6]

The various descriptions of this species invariably refer to "dark brown paraphyses" intermingled with or surrounding the spores. Burrill also records the same with regard to P. coronata. The bodies are easily found in both species by scraping off the pustules and examining the debris. But their varying tissue-like dimensions, dissimilarity to ordinary paraphyses (compare fig. 6*c* with fig. 7), and the further fact that they are always not only connected at the base with the stroma but also with the epidermis at the top, led me to believe that they could not be paraphyses in the best accepted sense, but were merely vertical extensions of the basal stroma. Furthermore, in all cases in which a microchemical reagent affected these bodies, the action was the same as that for the stroma.

Carefully prepared serial, vertical and tangential sections of the host leaves, passing through the pustules, confirmed the truth of this supposition.

Soon after the coalescence of the filaments which start the new sorus, the young spores appear, developing centrifugally, while the hyphæ which form the spore-bed eat away the host tissues, spread rapidly, and finally enclose the spores on the sides (fig. 2 *b* and *f*), thus, when fused together and with the epidermis at the top, cutting off what may be termed

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[4] For the use of the word see Sorauer, Pflanzenkrankheiten ed. 2, vol ii, p. 212. Also Plowright, "British Uredineæ and Ustilagineæ," p. 36.

[5] Vines, Physiology of Plants, p. 191.

[6] Saccardo, Sylloge Fungorum, vol. vii., part 2, p. 625.

a simple sorus. This development is well shown in the structure of the teleuto-pustule of P. anemones-virginianæ, the fusion of the stromal hyphæ often not being so complete as in other species (figs. 8 and 9). In this species the hyphæ are often seen in cross-section between the simple sori, showing that the vertical position taken by the hyphæ, as usually seen, is in a manner an enforced one, consequent upon the development of the sorus.

A further proof that these hyphæ are not different from the ordinary filaments is found in the fact that when not under pressure at the top they continue to elongate (fig. 8 *b*). The much thickened places on the covering of the pustules in this species are due to these same hyphæ which have passed through the epidermis, forming a fused mass, seen in section fig. 10 *c*. In all the sub-epidermal species on glumaceous plants the sori are found between the leaf-veins, becoming confluent in long lines, while the hyphæ which inclose the simple sori fuse to form the intersorial stromata (fig. 2 *c*) which in thick vertical sections of the compound sorus or pustule give the appearance of the intermixing with the spores of the so-called paraphyses of the descriptions. In vertical longitudinal sections of the pustule, these intersorial stromata are found to be formed across the space between the fibro-vascular bundles in great regularity of position. Whether these structures will be seen in vertical cross sections of the rust pustule depends wholly as to whether or not the space between the fibro-vascular bundles is wide enough for the development of two or more simple sori. From this it will be seen that the ordinary rust pustule of the sub-epidermal forms is not a simple structure as it appears from the exterior, but is compounded of many simple sori; and that the structures lying between owe their form and position merely to a crowding and fusing together of the hyphæ which separate the simple sori and are not separate bodies, paraphyses, but simply extensions of the spore-bed (stroma). That they generally appear as seen at *c* fig. 6 is because an optical section can not reveal the cellular structure. Because of the opacity of the walls and the smallness of the cavities, sections which are to make this structure plain must not have a thickness to exceed 10 $\mu$. In cross section the intersorial stromata appear as strips of regular tissue forming a net-work between the fibro-vascular bundles with which they are connected, while the spores fill up the intervening spaces (fig. 11 *c*). The only apparent difference between this fungal tissue and the host tissues into which it seems to graduate is its reddish brown color and its ability to resist the action of reagents, macerating fluids, etc.

That the teleutospores are sub-epidermal at maturity is apparently because of the fact that before they have become strong enough to rupture and throw off the epidermis the hyphæ which arise on the sides of the young sorus have fused with and hold that covering in place.

EXPLANATION OF PLATE XV.—Fig. 1. Vertical section through teleuto-sorus of *P. graminis* Pers. on leaf sheath of Triticum vulgare; host tissues in cross-section: *a*, epidermis; *b*, teleutospore; *c*, sclerenchyma; *d*, fungal hypha. × 120.

Fig. 2. Vertical transverse section of young compound teleuto-sorus of *P. coronata* Cda. on leaf of Avena sativa, showing the relation of the young spores to the surrounding tissues and the penetration of the host by the fungal hyphæ: *a*, epidermis; *b*, a portion of the spore-bed (stroma) in section; *c*, the same as found between the simple sori, a so-called paraphysis in vertical longitudinal section; *d*, young spores not yet septate; *e*, nearly mature spore; *f*, beginning of stroma which finally encloses the spores. × 350; section 5 $\mu$ thick.

Fig. 3. Portion of a vertical longitudinal section of leaf of Avena sativa, showing very early stage of a teleuto-sorus and intercellular hyphæ: *a*, epidermis; *b*, coalescing hyphæ forming the spore-bed; *c*, hypodermal cell.

Fig. 4. Tangential section of leaf of Avena sativa in hypodermal region passing through the young spore-beds: *a*, hypodermal cells; *b*, basal portions of young spores; *c*, intercellular hyphæ; *d*, hyphæ fused with cell walls and partly in section. Section 5 $\mu$ thick; ×350.

Fig. 5. Apices of four mature spores of *P. coronata* Cda. as seen from above, showing form and position of digitate processes. × 680.

Fig. 6. Spore and *so called paraphysis* in situ; typical form from *P. rubigo-vera* DC. on Hordeum jubatum: *a*, epidermis; *b*, teleutospore; *c*, the "*paraphysis*" (stroma). × 350.

Fig. 7. Two paraphyses from uredo-sorus of *Phragmidium rosæ-alpinæ* DC. × 350.

Fig. 8. Portion of a compound sorus of *P. anemones-virginianæ* Schw. on Anemone patens, showing intersorial stroma in section, *c-a*; *b*, hypha passing over apices of spores; *d*, hypha beneath the spore-bed; stroma and epidermis fused at *a*. × 200.

Fig. 9. Same as fig. 8; hyphæ which form the intersorial stroma not completely fused: *a*, epidermis; *b*, hypha; *c*, spore. × 200.

Fig. 10. Left corner of sorus of P. anemones-virginianæ: *a*, epidermis of host; *b*, hypha partly fused with epidermis; *c*, coalescing hyphæ; *d*, spore. × 200.

Fig. 11. Tangential section of leaf of Avena sativa cutting a compound sorus of P. coronata midway between spore-bed and epidermis: *a*, teleutospores in cross-section; *b*, cells of fibro-vascular bundle; *c*, intersorial stroma in cross-section. Section 5 $\mu$ thick. $\times$ 350.

Fig. 12. Teleutospores of P. rubigo-vera on Triticum vulgare from Ellis' "North American Fungi" No. 1471, showing variations in size and form upon the same host: *a*, *b*, type spores; *c* and *d*, spores bearing short points at apices; *f*, a one-celled spore. $\times$ 350.

Fig. 13. Teleutospores of *P. coronata* Cda. on Avena sativa from one host: *a* and *b*, type spores; *c*, *e* and *f*, forms often found; *d*, truncated spore; *g*, two mesospores and a teleutospore from corner of sorus. $\times$ 350.

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## Achenia of Coreopsis.

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(WITH PLATE XVI.)

Coreopsis shows as great a variety of achenia as any genus of Compositæ, but they are hard to define. They may be flat or somewhat 4-sided, straight or curved, orbicular to linear-oblong in outline, glabrous to pubescent, winged or wingless, with entire or laciniate-toothed margin, apex truncate or emarginate, pappus of two awns (sometimes more) or of teeth or scales, these generally upwardly hispid (often naked), or all these wanting. The genus is not clearly separated from Bidens, for while the one is said to have its awns always upwardly hispid, and the other downwardly hispid, several species in each hybridize freely and break down this distinction. While the genus possesses such a range of fruit structures, and by this alone one can not always distinguish species as now defined, it enables natural groups of a few species to be easily formed, and most of these can then be separated by leaf characters. In some cases it seems questionable whether these sub-divisions should be made, for they embrace so many intermediate forms that no line can be clearly drawn between them. No attempt has been made in this paper to combine species, with the belief that Dr. Gray in his Synoptical Flora has given the most satisfactory arrangement that can now be made. His lineal order has been followed in